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# *Rhizoglomus*, a new genus of the *Glomeraceae*

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Abstract — *Rhizoglomus* gen. nov. (*Glomeraceae*, *Glomeromycetes*) is proposed, typified by *Glomus intraradices* [≡ *Rhizoglomus intraradices*]. The genus encompasses species of arbuscular mycorrhizal fungi that frequently form abundant spores in soil and roots and is morphologically characterized by spores with cylindrical subtending hyphae (usually with an open pore at the base) and at least two or three (rarely up to five) distinct wall layers. Phylogenetically, the genus forms a separate clade in the *Glomeraceae*. In addition to *R. intraradices*, the genus includes *R. aggregatum, R. antarcticum, R. arabicum, R. clarum, R. custos, R. fasciculatum, R. invermaium, R. irregulare, R. manihotis, R. microaggregatum, R. natalense,* and *R. proliferum*. Some of these species were previously assigned to *Rhizophagus* (type: *R. populinus*), a pathogenic genus that does not belong in the *Glomeromycota*.

Key words — *Glomerales*, *Glomus aggregatum*, *Glomus clarum*, *Glomus fasciculatum*, *Glomus irregulare*

## Introduction

*Glomus* Tul. & C. Tul. s.l. (*Glomeraceae*, *Glomeromycetes*) comprises a heterogeneous assembly of arbuscular mycorrhizal (AM) fungi (e.g., Morton & Benny 1990, Schwarzott et al. 2001). In an attempt to redefine the genus more naturally, Schüßler & Walker (2010) reassigned several *Glomus* species characterized by the frequent formation of intraradical spores to *Rhizophagus* P.A. Dang. Dangeard (1896), who identified *Rhizophagus populinus* as the causal agent of a severe root disease of poplar (*Populus* spp.) in northern France,

later described the root infection structures of the species (Dangeard 1900) but neither designated nor deposited type specimens, as this was not the procedure at that time. Consequently, the vague type description (Dangeard 1896) and detailed drawings (Dangeard 1900) remain the only reference for *Rhizophagus* and its type species, *R. populinus*.

Several decades later, Gerdemann & Trappe (1974) synonymized *Rhizophagus* with *Glomus*. Later, reviewing the type description (Dangeard 1896), Schüßler & Walker (2010) noted, "examination of the protologue of *R. populinus* reveals that the species is an arbuscular mycorrhizal fungus that produces abundant spores in roots." For this reason they resurrected *Rhizophagus,* placing the genus in the *Glomeraceae.* Here, we argue that the name *Rhizophagus* should not be assigned to any species in the *Glomeromycota.*

First: Dangeard (1896) described (without providing any illustrations) a disease of poplar roots occurring under wet soil conditions, which produced "sporangia" and finely ramified hyphae inside the root epidermal cells. The morphology he observed led him to propose that the organism represented a new genus in the *Chytridineae*. He related the death of the poplar trees to this pathogen and not to a foliar disease. He did not observe germination of the "sporangia" but explained that there were durable spores or cysts in the root cells with a thick membrane and with protoplasm containing abundant oil. Dangeard (1896) did not describe that numerous spores (or sporangia or cysts) were formed in the infected poplar roots. The diagnosis of *Rhizophagus* therefore, published by Schüßler & Walker (2010), does not correspond with the observations described by Dangeard (1896).

Second: Dangeard (1900), through illustrations, showed that the infection structures of *R. populinus* in poplar roots comprised two structural types: i) those resembling vesicles (which he referred to as sporangia with dense protoplast) and ii) arbuscules (termed ramified hyphae in cells) of mycorrhizal root colonization. He did not recognize these structures as endomycorrhizae, however. He also illustrated spores, which were not connected to the vesicles or arbuscules. These spores were spherical, small (in relation to the root cells), and with an apparently single wall layer and one or two hyphal connections formed terminally or intercalary (see plate IX, D, E). Dangeard (1900) called these cells 'cysts' ('kystes' in French) because they contained a lipid globule. Recognizing these structures as characteristic of chytrids, Dangeard (1900) assigned *R. populinus* to the *Chytridineae*, a suborder containing root pathogenic fungi.

Third: Saccardo & Trotter (1912) transferred *Rhizophagus* to the *Peronosporaceae*[1] and stated that "sporae perdurantes intercalares v. terminales,

[1] In 1912 mycologists placed root-borne and root disease-causing fungi such as *Pythium* into the *Peronosporaceae* (see Middleton 1952, for historic overview). Today *Peronosporaceae* contain only foliar disease-causing fungi.

globosae, membrana levi et guttulis pluribus praeditae." Here, reference is clearly made to the lipid globules in the globose spores (also drawn by Dangeard (1900) in plate IX, Figs. D&E), a characteristic feature for spores of some representatives of the *Chytridiales* and *Oomycetes* (Hawksworth et al. 1983). Saccardo & Trotter (1912) referred to *R. populinus:* "Characteres generis. Hab. in radicibus junioribus Populi in Gallia occid. – Profunde penetrat et plantas necat," which clearly states that *R. populinus* causes death of the host plants. It must be noted, however, that early in the 20th century, fungal root pathogens were separated from *Peronosporaceae* and placed in families such as *Pythiaceae* (Middleton 1952). To our knowledge, no one ever officially transferred *Rhizophagus* to *Pythiaceae* or any other family in the *Oomycetes*.

Fourth: Petri (1919) argued that the structures depicted by Dangeard (1900) in poplar tree roots belonged to the endomycorrhizae and were vesicles and arbuscules, not the cause of death of the poplar trees. However, Petri ignored the cysts with lipid globules illustrated by Dangeard (1900). He believed that the poplar tree deaths in Northern France were resulted from a foliar disease and that *R. populinus* was not causing root disease.

Fifth: Butler (1939), who reviewed vesicular-arbuscular mycorrhizal fungi, showed that extramatrical fruiting bodies of *Endogonaceae* (including some species currently assigned to *Glomeraceae*) were connected with internal structures resembling those depicted by Dangeard (1900) that were later identified as vesicles and arbuscules. Butler concluded that the vesicles and arbuscules formed in roots represented the "imperfect form" of *Endogonaceae,* a form named by that Dangeard (1900) as *R. populinus*. His statement had far-reaching consequences: for a decade *Rhizophagus* was considered the most widely distributed fungus in the world, until Mosse (1953) successfully isolated the mycorrhizal spores and vesicular-arbuscular mycorrhizal structures from roots during inoculation experiments. Mosse (1953, 1970) showed that different spore "types" (i.e., species), such as "yellow vacuolated" and "honey-colored" spores, formed arbuscules and vesicles in roots.

Sixth: Gerdemann (1968) concluded, "...there is little reason to continue to use the name *Rhizophagus* [for a fungus forming vesicles and arbuscules in roots] ... as the genus *Endogone* was described much earlier." It should be noted that by 1968 vesicular-arbuscular mycorrhiza-forming fungi were organized in *Endogone* (*Endogonaceae*). A few years later Gerdemann & Trappe (1974) separated many species from the *Endogonaceae,* placing them into the genus *Glomus,* earlier described by Tulasne & Tulasne (1844). Following Gerdemann's (1968) reflections, the vesicles and arbuscules depicted by Dangeard (1900) could not be a morphological character restricted to *Rhizophagus,* as *Glomus, Sclerocystis* (described by Berkeley & Broome in 1873), and most other glomeromycete genera form such mycorrhizal structures.

Seventh: Gerdemann & Trappe (1974) synonymized *Rhizophagus* with *Glomus* without providing a specific justification, which is intriguing, given that Gerdemann (1968) had earlier doubted the validity of applying the name *R. populinus* to a vesicular-arbuscular fungal species. Indeed, at this point Gerdemann & Trappe (1974) should have eliminated the name *Rhizophagus* from the *Endogonaceae*.

Although Dangeard (1896, 1900) interpreted vesicles of a vesicular-arbuscular mycorrhizal fungus in poplar roots as sporangia, it is now clear that this was incorrect and that the spores (cysts) he described were not, in fact, released from these sporangia. This observation was also made after Schlicht (1889) had already described AM type endomycorrhizae and determined that numerous fungal species could be involved. It has since been established that AM vesicles and arbuscules are so morphologically uniform that they cannot be used to differentiate species, genera, families, or orders of in the *Glomeromycota* (Oehl et al. 2011a,b,c). Further, molecular techniques have demonstrated that single roots can be colonized simultaneously by numerous glomeromycete species (e.g., Lekberg et al. 2007, Tchabi et al. 2009, Borriello et al. 2012, Wetzel et al. 2014). Consequently, we assume that the vesicle and arbuscule structures delineated by Dangeard (1900) most likely resulted from combined infections of a number of species representing different orders of the *Glomeromycota*.

It is well established that poplar trees host non-pathogenic vesicular-arbuscular mycorrhizal fungi (Clark 1963), and it is likely that Dangeard (1900) observed such vesicles and arbuscules in poplar root cells in addition to spores of a disease-causing fungus such as *R. populinus*. Dehne (1982) and Linderman (1994) state that fungal root pathogens can occupy root cortical cells adjacent to those colonized by AM fungi, and that mycorrhizal colonization of a root can never confer complete immunity against any root disease (see Bagyaraj 1984). Such colonization by AM fungi in close vicinity of pathogens such as *Pythium* or *Rhizoctonia* has frequently been reported (e.g., Dehne 1982, Linderman 1994).

Additionally confusing, with respect to *Rhizophagus* and its type species, is that to date, no vesicular-arbuscular mycorrhiza-forming species of the *Glomeromycota* has been recorded as a root pathogen that kills a plant. This would represent a fundamental change to the current standing of vesicular-arbuscular mycorrhiza as the most widespread mutualistic symbiosis between flowering plants and soil-borne microorganisms.

It is actually quite remarkable that researchers and taxonomists have paid attention to only the vesicle and arbuscule structures described by Dangeard (1900) while after 1912 ignoring or overlooking the cysts he described (Dangeard 1896, 1900). According to our historical analysis, Dangeard (1900) described the real species in the last paragraph: "The cysts of *Rhizophagus populinus* are

spherical; the content is oily (P. IX, E); some even contain a large drop of oil (P. IX, D)." Saccardo & Trotter (1912) identified these cysts (spores) as the causal agent of a mortal poplar disease. Thus the actual *Rhizophagus populinus* cannot belong to the *Glomeromycota*, but rather represents *Oomycetes*.

We therefore conclude that the genus name *Rhizophagus* cannot be applied to a group of glomeromycotan fungi that form spores in plant roots, as suggested by Schüßler & Walker (2010). Hence, we propose a new genus, *Rhizoglomus*, to accommodate vesicular-arbuscular mycorrhizal fungal species of the *Glomeraceae* that often form abundant spores in the soil and roots of vascular plants.

## Materials & methods

Specimens and original species descriptions of ten *Glomus* spp., one *Endogone* sp., and two recently described *Rhizophagus* spp. (Symanczik et al. 2014, Błaszkowski et al. 2014) were re-examined. Type specimens, ex-type material (specimens or single species cultures either separated or propagated from original type material, and deposited at a herbarium or collection that was not mentioned in the protologue), and non-type specimens were provided by the herbaria OSC (Corvallis, Oregon), Z+ZT (Zurich), DEPE (Szczecin, Poland), URM (Recife, Brazil), Culture Collection of Vesicular-Arbuscular Mycorrhizal Fungi (INVAM), Swiss collection of Arbuscular mycorrhizal Fungi (SAF, Agroscope), and the private AM fungal collections of Sieverding, Oehl, and Błaszkowski. The Hall & Abbott (1979) photographic slide collection was also reviewed. For this paper, all original species descriptions and published species emendations were also considered.

Specimens were either mounted in lactophenol, in polyvinyl alcohol-lactic acid-glycerol (PVLG), in Melzer's reagent, in a mixture of PVLG + Melzer's reagent (1:1; Brundrett et al. 1994), in a mixture of lactic acid to water (1:1), or in water. When available, spores freshly isolated from soils or bait cultures were also mounted and analyzed. Spore wall terminology follows the nomenclature of Oehl et al. (2005, 2011b). Spore walls, germination structures, and all other mycorrhizal structures were investigated using a compound microscope at 100–1000× magnifications. All spore observations and all information on spore characteristics are based on spores extracted from soil, bait cultures, or single species cultures. No information is provided from in vitro-cultured material.

## Results

### Taxonomic analyses

***Rhizoglomus*** Sieverd., G.A. Silva & Oehl, **gen. nov.** Figs 1–15

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Differs from *Glomus* by regularly open pores at the spore bases, and usually wide open pore channels within the frequently cylindrical subtending hyphae.

Type species: *Glomus intraradices* N.C. Schenck & G.S. Sm. [≡ *Rhizoglomus intraradices*].

Etymology: from Latin: *rhiza* = root, referring to the often abundant hyphae, arbuscules, vesicles and spores formed in roots; and *Glomus*, referring to the genus in which the type species of *Rhizoglomus* was first described.

Spores formed in loose sporocarps, in clusters, or singly in soil, and frequently in roots. Wall of the subtending hyphae continuous with the spore wall, and for a certain distance concolorous with the spore wall, or slightly lighter in color. Subtending hypha cylindrical or seldom slightly funnel shaped at spore base. Pore at spore base regularly open, rarely closed by a septum. Spore walls show more than one, and generally two to three (and up to five) distinct layers, of which one or several of the outermost may separate when pressure is applied to spores. Forming vesicular-arbuscular mycorrhizae, whose fungal structures stain blue to dark blue in trypan blue.

**New combinations**

***Rhizoglomus aggregatum*** (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 803193

≡ *Glomus aggregatum* N.C. Schenck & G.S. Sm., Mycologia 74: 80. 1982.

Specimen examined: Type described from a pot culture by Schenck & Smith (1982). Isolated from Florida State near Haines City. Holotype OSC #40255, examined by Oehl at OSC in 2002.

***Rhizoglomus antarcticum*** (Cabello) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 803194

≡ *Glomus antarcticum* Cabello, Mycotaxon 51: 124. 1994.

Specimen examined: Type described from rhizospheric soil of *Dechampsia antarctica* at Danco Coast, Base Primavera, Antarctic Peninsula (Argentina), by Cabello et al. (1984). Specimen was loaned by M. Cabello to B.T. Goto (UFPE, Recife, Brazil) in 2009 and examined by Oehl at URM.

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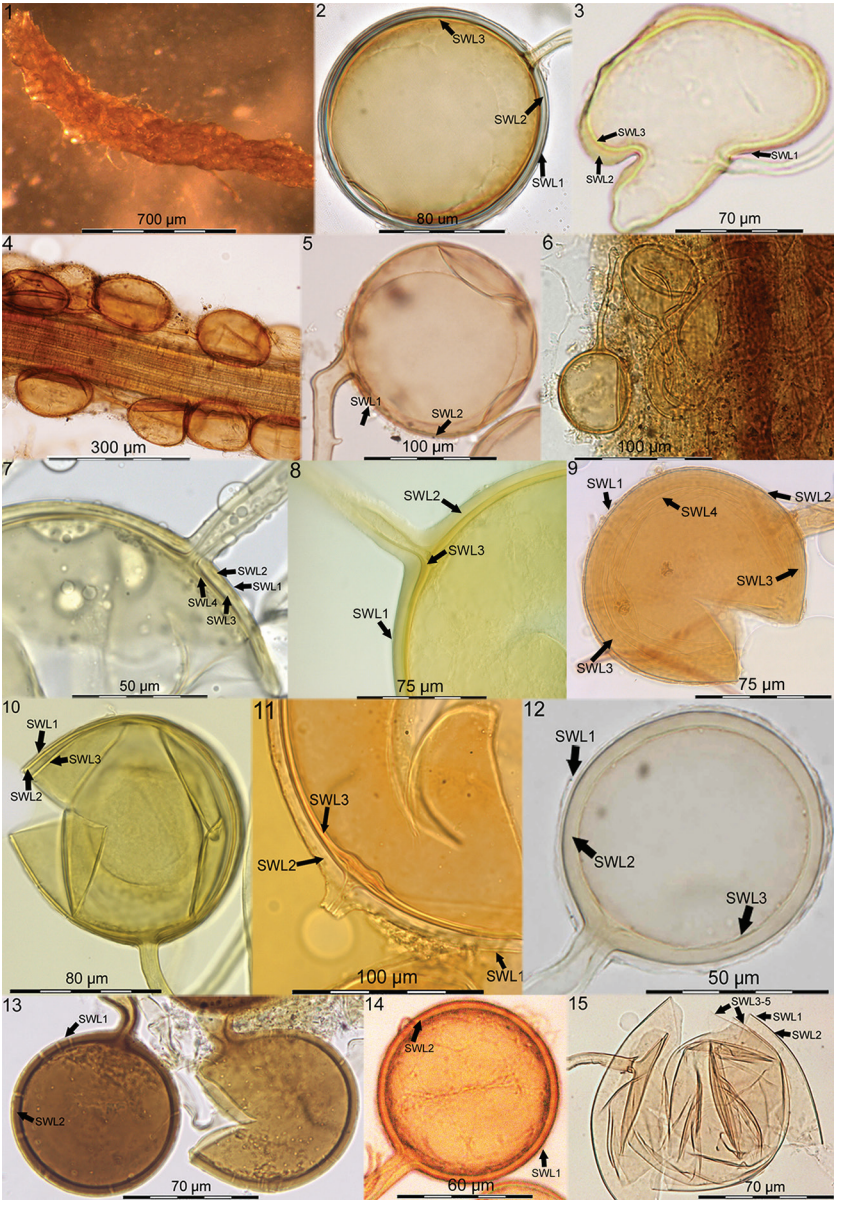
Figs 1–12. Spores of ***Rhizoglomus* spp.** from soils or within roots. ***Rhizoglomus intraradices*** (from Germany, ZT Myc 30479): **1.** Spores formed within the host root, isolated from pot culture. **2.** Spore with three wall layers (SWL1–3). ***Rhizoglomus irregulare*** (from Switzerland, ZT Myc 30483): **3.** Spore with three wall layers (SWL1–3). ***Rhizoglomus aggregatum*** (type, OSC): **4.** Spores formed within the host root. **5.** Spore with two wall layers (SWL1–2). ***Rhizoglomus microaggregatum*** (type, OSC): **6.** Spores formed within the host root; mature spores have two layers. ***Rhizoglomus proliferum*** (ex type, ZT Myc 30484): **7.** Spore with four wall layers (SWL1–4). ***Rhizoglomus clarum*** (from an INVAM culture): **8.** Spore with three wall layers (SWL1–3). ***Rhizoglomus natalense*** (from Natal, Brazil, isotype, DEPE 3384): **9.** Spore with four wall layers (SWL1–4). ***Rhizoglomus custos*** (ex type, ZT Myc 49021): **10.** Spore with three (SWL1–3) of four wall layers described visible. ***Rhizoglomus manihotis*** (from type, OSC): **11.** Spore with evanescent outer wall layer (SWL1), a rather thick hyaline layer (SWL2) and up to two separable yellow wall layers (SWL3). ***Rhizoglomus fasciculatum*** (from Switzerland, ZT Myc 30478): **12.** Spore with three wall layers (SWL1–3) and open pore. ***Rhizoglomus invermaium*** (isotype, OSC): **13.** Spores with two wall layers (SWL1–2).




***Rhizoglomus antarcticum*** (from type, M. Cabello collection): **14.** Spore with two (SWL1–2) layers visible (of three described). ***Rhizoglomus arabicum*** (isotype, DEPE): **15.** Spore with 2–5 wall layers, depending on layer and laminae definition, not easily discerned.

***Rhizoglomus arabicum*** (Błaszk., Symanczik & Al-Yahya'ei) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 809436

≡ *Rhizophagus arabicus* Błaszk., Symanczik & Al-Yahya'ei, Mycologia 106: 253. 2014.

Specimen examined: Type described from two pot cultures by Symanczik et al. (2014). Isolated from an undisturbed natural field at Al-Kamel in Al-Sharqyia region of Oman; examined by Oehl in 2014. One slide deposited at Z+ZT (ZT Myc 57169).

***Rhizoglomus clarum*** (T.H. Nicolson & N.C. Schenck) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 803195

≡ *Glomus clarum* T.H. Nicolson & N.C. Schenck, Mycologia 71: 182. 1979.
≡ *Rhizophagus clarus* (T.H. Nicolson & N.C. Schenck) C. Walker & A. Schüssler, The *Glomeromycota*: 19. 2010.

Specimen examined: Type described from a pot culture by Nicolson & Schenck (1979) from soil on the Agronomy Farm of the University of Florida. Type at OSC, examined by Oehl at OSC in 2002, and by Sieverding at Centro Internacional de Agricultura Tropical (CIAT; Cali, Colombia) culture collection.

***Rhizoglomus custos*** (C. Cano & Dalpé) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 803196

≡ *Glomus custos* C. Cano & Dalpé, Mycotaxon 109: 502. 2009.
≡ *Rhizophagus custos* (C. Cano & Dalpé) C. Walker & A. Schüssler, The *Glomeromycota*: 19. 2010.

Specimen examined: Ex type specimens (Cano et al. 2009) isolated from cultures maintained at EEZ, CSIC in Granada, Spain (collection date 15.9.2013 by J. Palenzuela; ZT Myc 49021; examined by Oehl).

***Rhizoglomus fasciculatum*** (Thaxt.) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 803197

≡ *Endogone fasciculata* Thaxt., Proc. Am. Acad. Arts & Sci. 57: 308. 1922.
≡ *Glomus fasciculatum* (Thaxt.) Gerd. & Trappe, Mycol. Mem. 5: 51. 1974.
≡ *Rhizophagus fasciculatus* (Thaxt.) C. Walker & A. Schüssler, The *Glomeromycota*: 19. 2010.
= *Endogone arenacea* Thaxt., Proc. Am. Acad. Arts & Sci. 57: 317. 1922
= *Rhizophagites butleri* Rosend., Bull. Torrey Bot. Club 70: 131. 1943.

Specimen examined: Non-type specimen (morphology following Thaxter 1922; sensu Walker & Koske 1987) collected in bait cultures from Switzerland, near Basel (collection date 1.10.2005); examined by Oehl (ZT Myc 30478).

***Rhizoglomus intraradices*** (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 803192

≡ *Glomus intraradices* N.C. Schenck & G.S. Sm., Mycologia 74: 78. 1982.
≡ *Rhizophagus intraradices* (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüssler, The *Glomeromycota*: 19. 2010.

Specimen examined: Type described from a pot culture by Schenck & Smith (1982). Isolated from Florida State at the USDA Horticultural Research Station in Orlando. Type OSC #40255, examined by Oehl at OSC in 2002. Non-type from a pot culture (SAF51) established by Oehl, isolated from a temporary *Lolium perenne* grassland in Biengen (Germany), near Freiburg im Breisgau (ZT Myc 30479); examined by Oehl.

***Rhizoglomus invermaium*** (I.R. Hall) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 808609

≡ *Glomus invermaium* I.R. Hall, Trans. Br. Mycol. Soc. 68: 345. 1977.

Specimen examined: Isotypes after Hall (1977) deposited at OSC #43941. Hall & Abbott (1979) photographic slide collection representing the type specimens deposited at PDD herbarium; examined by Oehl. Several greenhouse pot cultures of *Gl. invermaium*, established from single spores on host plant *Hieracium pilosella* (so-called monosporic cultures) at SAF (see http://www.agroscope.admin.ch/bodenoekologie/08050/08067/08068/index.html?lang=en; accessions SAF205-208) were examined. Specimens from three cultures were deposited at Z+ZT (ZT Myc 57170-57172), and first sequences from these cultures at EMBL-EBI (LN624111-LN6241112; Säle et al., unpublished).

***Rhizoglomus irregulare*** (Błaszk., Wubet, Renker & Buscot) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 803198

≡ *Glomus irregulare* Błaszk., Wubet, Renker & Buscot, Mycotaxon 106: 252. 2009.

≡ *Rhizophagus irregularis* (Błaszk., Wubet, Renker & Buscot) C. Walker & A. Schüssler, The *Glomeromycota*: 19. 2010.

Specimen examined: Type described from a pot culture by Błaszkowski et al. (2009). Isolated from Poland near Szczecin. Type (DPP, nowadays DEPE). Type specimen examined by Oehl at SAF from a type culture maintained in Basel in 2008 (ZT Myc 30480). Non-types from pot cultures established by Oehl. Isolated from three Swiss long-term experiments in Therwil near Basel, in Frick and in Zollikofen near Bern, respectively (ZT Myc 30481; ZT Myc 30482 and ZT Myc 30483); examined by Oehl in 2008-2014.

***Rhizoglomus manihotis*** (R.H. Howeler, Sieverd. & N.C. Schenck) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 803199

≡ *Glomus manihotis* R.H. Howeler, Sieverd. & N.C. Schenck, Mycologia 76: 695. 1984.

≡ *Rhizophagus manihotis* (R.H. Howeler, Sieverd. & N.C. Schenck) C. Walker & A. Schüssler, The *Glomeromycota*: 19. 2010.

Specimen examined: Type described from a pot culture on *Pueraria phaseoloides* (Roxb.) Benth. by Schenck et al. (1984). Isolated from Colombia near Quilichao (Cauca). Type OSC #41495, #41498, specimen examined by Oehl at OSC in 2002, and by Sieverding who cultivated the type under the accession C-1-1 at CIAT (ZT Myc 30484).

***Rhizoglomus microaggregatum*** (Koske, Gemma & P.D. Olexia) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 803200

≡ *Glomus microaggregatum* Koske, Gemma & P.D. Olexia, Mycotaxon 26: 125. 1986.

Specimen examined: Holotype described from soil by Koske et al. (1986) from USA, Michigan, Benzie Co. Holotype OSC #46719; examined by Oehl at OSC in 2002.

***Rhizoglomus natalense*** (Błaszk., Chwat & B.T. Goto) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 810477

≡ *Rhizophagus natalensis* Błaszk., Chwat & B.T. Goto, Mycotaxon 129: 100. 2014.

Specimen examined: Type described from pot-cultured *Plantago lanceolata* by Błaszkowski et al. (2014). Isolated from a sand dune in Parque Estadual das Dunas de Natal "Journalista Luiz Maria Alves" (Rio Grande do Norte, Brazil); examined by Oehl in 2014. One slide deposited at URM (URM 87580).

***Rhizoglomus proliferum*** (Dalpé & Declerck) Sieverd., G.A. Silva & Oehl **comb. nov.**

MycoBank MB 803201

≡ *Glomus proliferum* Dalpé & Declerck, Mycologia 92: 1180. 2000.

≡ *Rhizophagus proliferus* (Dalpé & Declerck) C. Walker & A. Schüssler, The *Glomeromycota*: 19. 2010.

Specimen examined: Type described from monoxenic culture by Declerck et al. (2000) from Neufchateau, Guadeloupe, France. Isotype MUCL 41827, examined by Oehl from a pot culture maintained in Basel in 2008 (ZT Myc 30485).

Some species that superficially resemble *Rhizoglomus* species (e.g., *G. diaphanum*, *G. pallidum*, and *G. vesiculiferum*) were not considered, as their spore formation might differ from that of *Rhizoglomus* and their molecular phylogeny has not yet been fully determined or remains unclear.

## Discussion

The name of the new genus, *Rhizoglomus,* is based on the ability of its species to form abundant spores, spore clusters, or sporocarps in the bulk soil and soil rhizosphere and additionally within roots. Formation of spores within roots of host plants is, however, not unique to *Rhizoglomus*. Certain species of other, phylogenetically distant, genera also form spores inside roots, e.g., *Claroideoglomus lamellosum* (Dalpé et al. 1992, as *Glomus lamellosum*), *Septoglomus xanthium* (Błaszkowski et al. 2004, as *G. xanthium*), *Archaeospora myriocarpa* (Schenck et al. 1986, as *Acaulospora myriocarpa*), and *Entrophospora infrequens* (Sieverding & Toro 1985, Sieverding & Oehl 2006).

*Rhizoglomus* species, however, differ from other *Glomeraceae* (sensu Oehl et al. 2011a,b) in that they possess a pore or channel that is usually open at the connection between spore and the cylindric subtending hypha. One or a few septa may form in the hyphae at some distance from the spore base. Mature spores of most *Rhizoglomus* spp. have two or up to five distinct layers of which one to three hyaline to subhyaline outer layers may separate from the inner, persistent (= structural), and usually pigmented layer(s) when spores are squeezed. In some species, such as *R. intraradices* and *R. irregulare,* the

outer hyaline to subhyaline layers may degrade or slough away from the inner persistent layer(s).

In spores of *Glomus* spp., the basal channel or pore is generally obstructed by wall material or proper septa (Oehl et al. 2011b). In *Funneliformis*, the hyphal attachment is characteristically funnel-shaped (Oehl et al. 2011b). *Simiglomus* resembles *Rhizoglomus* in its similarly open-pored hyphal attachment, but its hyphal walls are substantially thicker and thicken over longer distances than in *Rhizoglomus*. *Septoglomus* spp. have regular septa or strong plugs at the spore base (Oehl et al. 2011b). The taxonomic separation of *Rhizoglomus* based on morphological characteristics was corroborated by molecular studies that placed *Rhizoglomus* spp. in a separate clade (Schüßler & Walker 2010, Krüger et al. 2012); this clade was formerly called the „*Glomus* group Ab2" (Oehl et al. 2011b).

To date, no *Rhizoglomus* species has been reported to cause a root disease resulting in the dieback or death of a plant. *Rhizoglomus* comprises 'key species' of AM fungi with regard to scientific and economic importance, such as *R. intraradices* and *R. irregulare* (e.g., Stockinger et al. 2010). The latter, formerly often confused with *R. intraradices* (Stockinger et al. 2010), develops well on axenic root cultures (Chabot et al. 1992) and has therefore been used as a model organism for AM fungal genetics (e.g., Jansa et al. 2002, Börstler et al. 2008, Croll et al. 2008, 2009). These AM fungi are also key components of many of the commercially available AM fungal products. Further from our extensive re-examination, both morphologically and molecularly, of the various specimens and cultures and our re-evaluation of the literature, we are convinced that such important AM fungal species should be placed correctly in *Glomeromycota* and not erroneously assigned to a pathogenic genus, such as *Rhizophagus*.

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